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Retinal Illuminance and Contrast Sensitivity in Human Infants

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Several investigators have related infants' low contrast sensitivity to immaturities in the optics and receptor lattice of the immature eye. A critical element in the modeling is how much the lower photon catch of the immature retina reduces sensitivity; the assumptions vary from square-root to Weber's law and lead to very different modeling outcomes. We measured the relationship between retinal illuminance and contrast sensitivity at different spatial frequencies. The sweep visual-evoked potential was used to measure thresholds in 2- and 3-month olds and adults over a 2.5-log-unit range of illuminances. The contrast threshold vs illuminance functions were fit by power functions. The best-fitting exponents for adults were about −0.5 at higher spatial frequencies (consistent with square-root law) and lower at lower frequencies. The best-fitting exponents for 2- and 3-month olds were −0.2 to −0.35 which indicates that threshold is less affected by changes in illuminance than is the case in adults. These results suggest that none of the models relating optical and receptoral immaturities to infants' spatial vision has assumed an appropriate relationship between lower photon catch and contrast sensitivity. Once the models are modified to incorporate the relationship obtained in the present experiment, the predictions fall well short of explaining 2-month olds' low contrast sensitivity.

Contrast sensitivity   Human infants   Visual acuity

INTRODUCTION

The spatial vision of young infants is quite limited compared to adults' (Banks & Salapatek, 1983; Braddick & Atkinson, 1988). For example, neonates' contrast sensitivity is at least an order of magnitude lower than adults' even at the peak of the age-appropriate contrast sensitivity function (CSF) (Atkinson, Braddick, & Moar, 1977; Banks & Salapatek, 1978; Norcia, Tyler, & Hamer, 1990). We also know that the neonatal retina is distinctly immature. Foveal and parafoveal cones are widely spaced and individually ineffective at absorbing photons (Abramov, Gordon, Hendrickson, Hainline, Dobson, & LaBossiere, 1982; Yuodelis & Hendrickson, 1986); peripheral cones are more mature but still not adult-like (Hendrickson & Drucker, 1992). A consequence of this retinal immaturity is reduced photon catch. By one estimate, the neonate's foveal cone lattice absorbs incoming photons at a rate of 1/350 compared to the adult's foveal lattice (Banks & Bennett, 1988). The lower catch is, in a sense, similar to the effect of reducing retinal illuminance by placing dark glasses in front of the eye.

If the reduced photon catch were the only difference between neonates and adults, their contrast sensitivities could be equated by increasing the light level presented to infants enough to overcome the attenuation of the theoretical glasses. This view of the development of spatial vision has been called the *dark glasses hypothesis* (Brown, Dobson, & Maier, 1987; MacLeod, 1978). Allen, Bennett, and Banks (1992), Brown *et al.* (1987), and Dobson, Salem, and Carson (1983) have shown that the dark glasses hypothesis fails to explain the poor visual acuity of 1- to 2-month-old infants. Specifically, they showed that infants' grating acuity is still significantly lower than adults' even when the retinal illuminance presented to infants was 2 or more log units higher than the illuminance presented to adults.

These results rule out the dark glasses hypothesis as the sole explanation of infants' low visual resolution. Indeed, the reduced photon catch of the infant retina is not even the most significant deficit (Allen *et al.*, 1992). This observation is not surprising, however, because at least three factors besides photon catch limit visual acuity and all three factors are likely to change with age. First, receptor spacing sets a limit to the highest resolvable spatial frequency, the so-called Nyquist limit (Williams, 1985), and the receptors of the young retina are significantly more widely spaced than those of the adult retina (Banks & Bennett, 1988; Yuodelis &

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Hendrickson, 1986). Second, the quality of the eye's optics limits its ability to transmit fine detail into the retinal image (Campbell & Gubisch, 1966), and the optical transfer function of the infant's eye is unknown. Moreover, infants' accommodation is uncontrolled and notoriously inaccurate in nearly all experiments (Banks, 1980; Dobson, Howland, Moss, & Banks, 1983; Haynes, White, & Held, 1965), so infants' retinal images may be optically degraded in most experimental situations. Because optical defocus has its largest effect at high spatial frequencies, acuity measurements are more affected by poor optics and inaccurate accommodation than are other measurements such as low- and medium-frequency contrast sensitivity (Green & Campbell, 1965). Third, post-receptoral convergence of receptors onto higher-order retinal neurons acts as a low-pass filter attenuating responses to high spatial frequencies (Banks & Crowell, 1995; Wilson, 1988, 1995); again the effect is larger for acuity measurements than for low- and medium-frequency contrast sensitivity. For these reasons, the failure of a reduced photon catch model to explain infants' coarse visual resolution does not rule out reduced catch as a major constraint on performance in other visual tasks such as contrast sensitivity. To test the effect of retinal illuminance on contrast sensitivity, measurements of the relationship between light level and sensitivity are required at the ages of interest.

Models of the effects of reduced photon catch on infant spatial vision require an assumption of how much contrast sensitivity ought to change for a given loss of photons. Three different models relating retinal immaturity to spatial visual sensitivity make rather divergent predictions concerning the relationship between illuminance and contrast sensitivity. At one extreme, Wilson (1988, 1995) assumed that infants' contrast sensitivity follows square-root law, so a 1-log-unit deficit in photon catch ought to produce a 0.5-log-unit deficit in contrast sensitivity for all spatial frequencies. At the other extreme, Brown (1990) assumed that infants' increment sensitivity follows Weber's law at the illuminances normally presented in infant experiments, so large reductions in photon catch ought to have no effect on sensitivity. Between those two extremes, Banks and Bennett (1988) assumed that the illuminance dependence of contrast sensitivity in infants was similar to adults; thus, contrast sensitivity should follow square-root law at moderate photopic luminances for spatial frequencies of 5 c/deg and above (van Nes & Bouman, 1967; Banks, Geisler, & Bennett, 1987).

Finally, it has been suggested that spatially-tuned mechanisms are present early in life (Banks, Stephens, & Hartmann, 1985; Wilson, 1988, 1995), and that their preferred spatial frequencies shift to higher values with age as cones in the central retina migrate centripetally. Wilson hypothesized that preferred frequency increases 4.5-fold from birth to maturity. In other words, a mechanism tuned to 1 c/deg at birth will be tuned to roughly 4.5 c/deg later on. If this is so, one might expect a 1-c/deg mechanism in newborns to operate more similarly to a 4.5-c/deg than to a 1-c/deg mechanism in adults. For example, 1- and 4.5-c/deg mechanisms may be affected more similarly by changes in illuminance than mechanisms preferring the same spatial frequency. However, if this prediction was disconfirmed, it would not necessarily contradict Wilson's hypothesis because the adaptive properties of these mechanisms could also change with age.

A handful of experiments have examined the relationship between increment threshold and illuminance and found that infants' threshold vs intensity curves are generally shallower than adults' at photopic illuminances (Dannemiller & Banks, 1983; Hansen & Fulton, 1981). Because these experiments used small test spots, one cannot determine from these reports how contrast sensitivity at different spatial frequencies depends on photon catch. There are two reports in the literature concerning infants' CSFs at different illuminances. Banks and Salapatek (1981) measured CSFs at two luminances (55 and 9.2 cd/m^2) using the forced-choice preferential-looking procedure; six 2-month olds were tested at the higher luminance and seven at the lower. Fiorentini, Pirchio, and Spinelli (1980) also measured CSFs at two luminances (6 and 0.06 cd/m^2) using a visual-evoked potential (VEP) technique; only one infant was tested at ages of 2.5, 4, and 7 months. Both of these experiments are limited because of the range of illuminances tested in the one case and the small number of subjects tested in the other.

The experiment reported here was expressly designed to address the above-mentioned issues. We measured contrast sensitivity as a function of retinal illuminance in 2- and 3-month-old infants using a swept-parameter, VEP technique.

METHODS

Subjects

Infants were recruited by letter and phone from county birth records. After receiving informed consent from their parents, 15 2-month-olds (post-natal ages 51–74 days) and 12 3-month-olds (87–103 days) were tested. All were born within 2 weeks of due date according to the birth record and none had significant health problems. Nearly all were examined with near retinoscopy (Mohindra, 1977) and a cover test. None displayed significant refractive error, media opacity, or strabismus. In testing an individual child, we randomly chose a spatial frequency and then attempted to obtain thresholds at three luminances. If those thresholds were measured successfully, we chose another spatial frequency and again attempted to obtain thresholds at three luminances. The data from one 2-month old were excluded because of consistently poor signal-to-noise ratios in the VEP. One-3-month old was dropped from the experiment because of fussiness. Three to four sessions were required to complete testing on each child. None of the infants was able to complete all nine spatial frequency by luminance conditions within the allotted number of sessions. Nonetheless, all of the infants, except one 2-month old, provided at least three thresholds at a minimum of one spatial frequency.

We also tested four adults, including two authors, with normal corrected acuity.

Stimuli

Vertical black/white sinusoidal gratings, counterphase-reversed at 6 Hz (square-wave modulation), were displayed on a Conrac 7300 color monitor controlled by a Rastertech One/80 graphics processor. The room was otherwise dark. The visible part of the display was rectangular subtending 50 × 40 deg at the 30-cm viewing distance. Two-month olds were presented spatial frequencies of 0.15, 0.3, 0.65, 1.2, and 2.2 c/deg; 3-month olds were presented 1.1, 2.2, and 4.3 c/deg. Adults were tested at 100 and 200 cm and were presented spatial frequencies of 0.5, 1, 2, 4, and 8 c/deg.

The Rastertech display was limited to 8 bits grayscale, so we changed stimulus luminance by placing neutral filters in front of the display. The space-average luminances presented to infants were 0.11, 2.8, and 70 cd/m^2, a range of 2.5 log units (values of 0.56 and 14 cd/m^2 were also presented to the adults). All luminances and contrasts were measured periodically with a Pritchard photometer. A software look-up table was modified whenever the calibration changed.

Procedure

Before every experimental run, the infant subject was adapted to the appropriate luminance for at least 8 min while informed consent was being obtained and the electrodes were being attached. Adaptation was achieved by placing the infant in a section of the room with uniform walls and adjustable illumination. The child was then exposed to a uniform display screen of the appropriate luminance for an additional 2 min; fixation was encouraged by use of noise-making toys dangled in front of the screen. Testing at one illuminance was completed before beginning another. Similar care was taken to insure that adult subjects were adapted to the appropriate luminance before testing was begun.

During testing, the child was seated on a parent's lap. One experimenter monitored the infant and used noise-making toys to engage the child's attention and to hold fixation on the center of the screen. A second experimenter monitored the EEG. Either experimenter could terminate a trial and would do so whenever attention waned, fixation shifted off the screen, or the EEG exhibited movement artifacts.

Contrast thresholds were estimated using the sweep VEP technique described by Norcia and Tyler (1985). Electrode placement for infants was 1 cm above the inion (reference), 3 cm to the left and right (recording), and top of the head (ground). The reference was 3 cm above the inion for adults. A soft elastic headband held the electrodes in place. The electrodes were connected via isolation cables to Grass P511 EEG amplifiers. The bandwidths of the amplifiers were 1–100 Hz and their gains were set to 10,000. An 8-bit D/A converter with self-ranging adjustment digitized the EEG waveform at 180 Hz. For each VEP run, the spatial frequency of the stimulus was fixed and the contrast was increased in 19 equal logarithmic steps, once every 500 msec. Typically, contrast was increased by 1 log unit during such a sweep. For infants, the initial contrasts were 2–8% depending on the spatial frequency and luminance. For adults, the initial values were 0.4–1.6%. At least five 10-sec trials were recorded and averaged for each condition. The VEP amplitude and phase of the second harmonic were extracted from the EEG using a discrete Fourier transform algorithm (Norcia & Tyler, 1985). A regression line was fit to a plot of response amplitude vs log stimulus contrast using both signal-to-noise ratio and phase consistency criteria (see Norcia, Clarke & Tyler, 1985, for details). The response signal amplitude had to exceed the noise amplitude by 0.5 log units. In portions of the record used for the regression, there could be no local EEG transients that elevated the amplitude of the noise frequency to more than 70% of that at the response frequency. The phase of the response had to be either constant or gradually leading the stimulus as contrast increased. Intersection of the regression line with 0 μV was taken as the contrast threshold. The threshold estimates were always obtained from the vector-averaged regression lines; i.e. lines were never fit to the data by hand.

Four adults were tested using the same stimuli and procedure. In addition, two of them were tested psychophysically using the same stimuli. Psychophysical thresholds were estimated using a two-interval, forced-choice procedure and the method of constant stimuli.

To calculate retinal illuminances, estimates of pupil diameter in the experimental setting were required. Thus, we videotaped the sessions of two 2-month olds and two adults. The face was illuminated by the display screen and an infrared light source. A small paper ruler was attached to the subject's forehead so we could calibrate the measurements. Pupil diameters were measured by hand during replays of the video.

RESULTS

Pupil measurements

Pupil diameter was measured in the experimental situation for space-average luminances of 0.11, 2.8, and

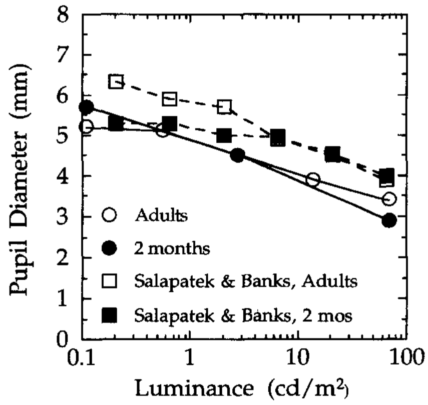

FIGURE 1. Pupil diameter as a function of luminance. Average pupil diameters in the present study and in Salapatek and Banks (1978) are plotted for 2-month olds and adults.

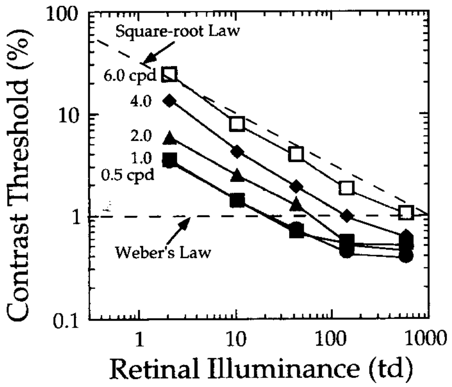

FIGURE 2. Adult contrast threshold as a function of retinal illuminance measured psychophysically. The data points represent averages from two adults at spatial frequencies ranging from 0.5 to 6 c/deg. Thresholds were obtained using two-interval, forced-choice procedure and the method of constant stimuli. Square-root and Weber's law are indicated by the dashed lines with slopes of −0.5 and 0.0 respectively.

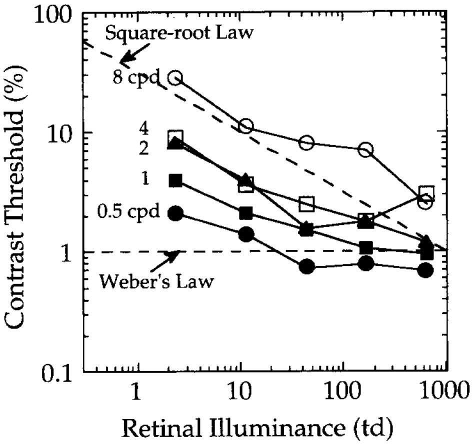

FIGURE 3. Adult contrast threshold as a function of retinal illuminance measured electrophysiologically. The data points represent averages from four adults at spatial frequencies ranging from 0.5 to 8 c/deg. Thresholds were obtained using the sweep VEP technique. Square-root and Weber's law are indicated by the dashed lines.

70 cd/m^2 (values of 0.56 and 14 cd/m^2 were also presented to the adults). Figure 1 displays the average pupil diameters for two 2-month olds and four adults as a function of luminance along with 2-month data from Salapatek and Banks (1978). There are only small differences among these data; pupil diameter in all three data sets decreases monotonically from 5–6 mm at 0.1–0.2 cd/m^2 to 2.5–3.5 mm at the highest luminances.

For an adult eye, retinal illuminance in trolands (td) is defined as the product of the pupil area (in mm^2) and stimulus luminance (in cd/m^2). Infant eyes are smaller than adult eyes, so the light from a stimulus is concentrated on a smaller retinal region. To take account of this, we calculated retinal illuminance in equivalent trolands by the following formula:

$$td_e = A * L * (f_a/f_i)^2$$

where td_e is retinal illuminance in equivalent trolands, A is pupil area in mm^2, L is stimulus luminance in cd/m^2 and f_i and f_a are the focal lengths of infant and adult eyes respectively. The ratio f_a/f_i is roughly 1.43 in 2- to

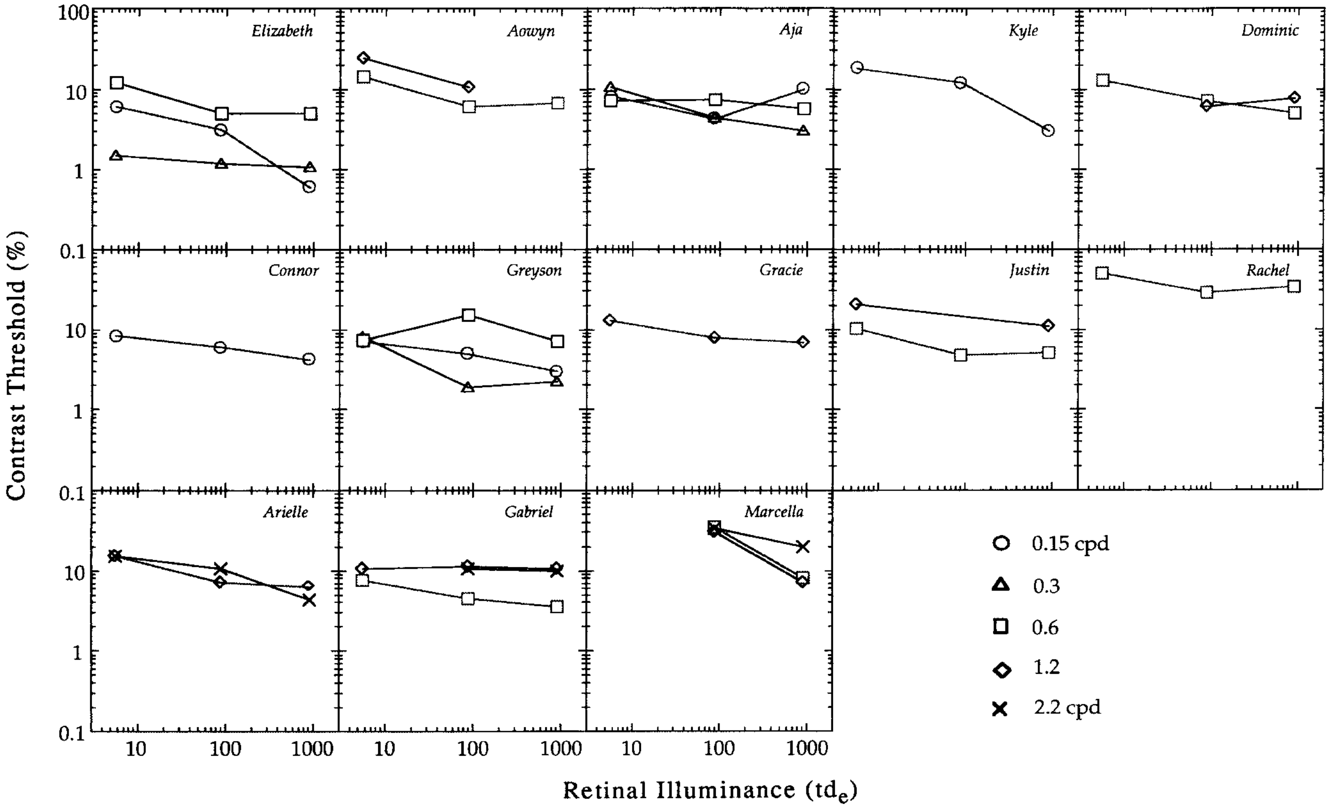

FIGURE 4. Individual 2-month data. Contrast thresholds obtained with the sweep VEP are plotted as a function of retinal illuminance. The horizontal axis represents equivalent trolands (see Methods). ○: thresholds at 0.15 c/deg; △: 0.3 c/deg; □: 0.6 c/deg; ◇: 1.2 c/deg; ×: 2.2 c/deg.

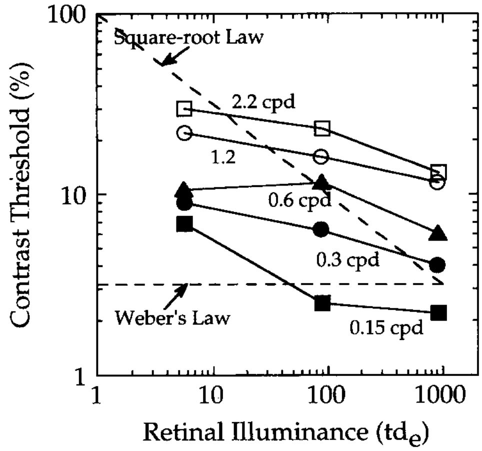

FIGURE 5. Average 2-month data. Average contrast thresholds are plotted as a function of retinal illuminance. The horizontal axis represents equivalent trolands. The data points represent averages from 13 two-month olds at spatial frequencies ranging from 0.15 to 2.2 c/deg. Square-root and Weber's law are indicated by the dashed lines.

3-month olds (Banks & Bennett, 1988; Larsen, 1971). Using this formula, we estimate retinal illuminances in 2- to 3-month infants (in equivalent photopic trolands) as 5.73, 88.8, and 911 for stimulus luminances of 0.11, 2.8, and 70 cd/m^2 respectively.

Adult contrast threshold measurements

Figure 2 shows the contrast thresholds obtained psychophysically from two of the adult observers. Average threshold is plotted as a function of retinal illuminance for a variety of spatial frequencies. The two dashed lines represent square-root and Weber's law. As expected (e.g. van Nes & Bouman, 1967; Koenderink, Bouman, Bueno de Mesquita & Slappendel, 1978), the data at higher spatial frequencies and lower luminances followed Weber's law, but as spatial frequency decreased or illuminance increased, the variation in threshold with changes in illumination lessened, thus approximating Weber's law behavior.

Contrast thresholds were also obtained using the sweep VEP procedure for each combination of spatial frequency and luminance in four adult observers. Figure 3 displays average contrast thresholds as a function of retinal illuminance for the five spatial frequencies presented. Again, the dashed lines represent square-root and Weber's law.

The adult psychophysical and VEP data in these two figures are quite similar, particularly with respect to the effect of retinal illuminance. This similarity between existing adult psychophysical results and our adult VEP results helps validate our procedure for estimating contrast thresholds.

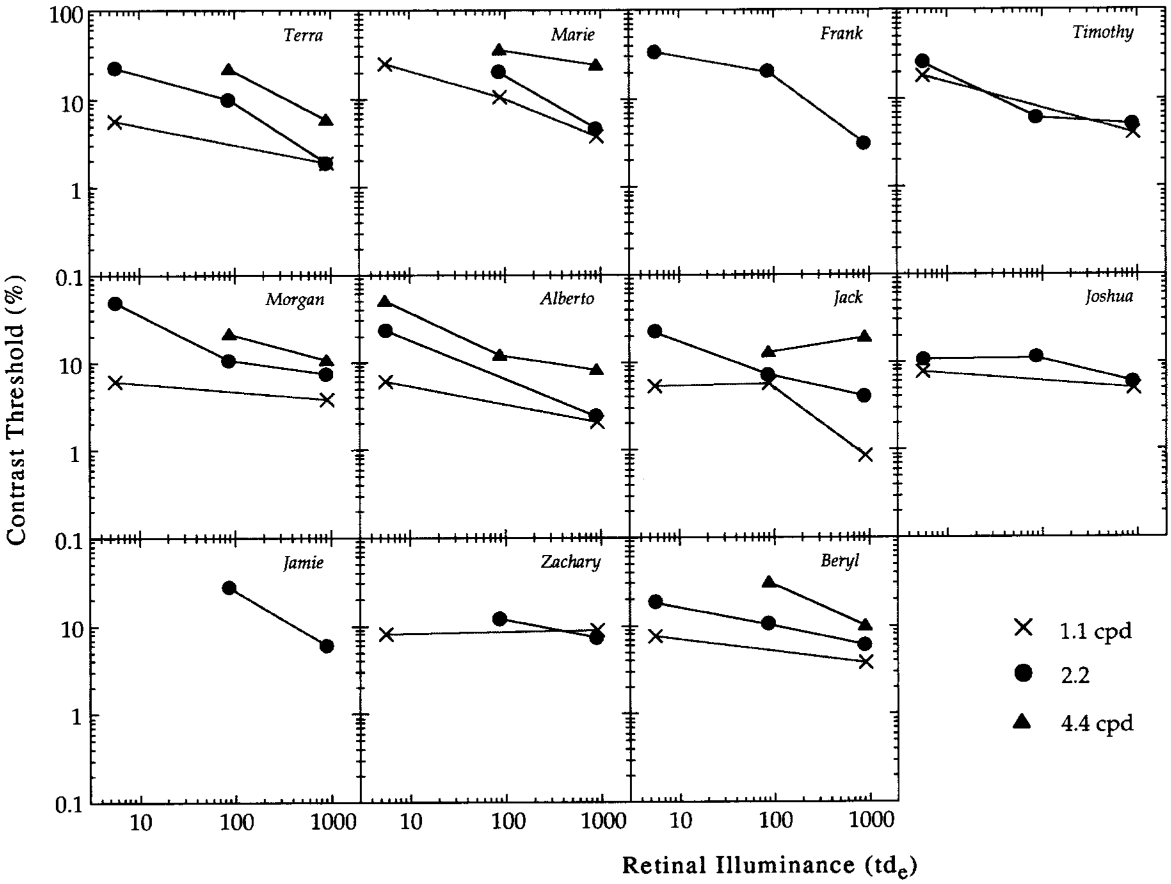

FIGURE 6. Individual 3-month data. Contrast thresholds obtained with the sweep VEP are plotted as a function of retinal illuminance. The horizontal axis represents equivalent trolands (see Methods). ×: thresholds at 1.1 c/deg; ●: 2.2 c/deg; ▲: 4.4 c/deg.

Infant contrast threshold measurements

The same contrast threshold vs illuminance functions were measured in 13 2-month olds and 11 3-month olds. Figure 4 displays the 2-month individual subject data.

Figure 5 displays the average 2-month data. The data points represent the geometric means of all thresholds obtained at the combinations of spatial frequency and illuminance indicated. Standard deviations of the data points in Fig. 5 were 0.09–0.47 log units. We also computed geometric means when individual subjects who did not provide complete data sets were omitted and the resultant did not differ significantly. The figure shows that threshold dropped with increasing illuminance for all spatial frequencies tested, so Weber's law did not hold for these conditions. The slopes of the contrast-threshold vs illuminance functions were, however, shallower than predicted by square-root law.

Figure 6 displays the 3-month individual subject data. All but two of these infants provided three thresholds at a minimum of one spatial frequency. Figure 7 displays the average 3-month data. Again the data points represent the geometric means of all thresholds obtained and similar functions were obtained if we omitted incomplete data sets. Standard deviations of the points in Fig. 7 ranged from 0.17 to 0.30 log units. As with the 2-month data, threshold dropped with increasing illuminance for all spatial frequencies. Neither Weber's law nor square-root law provided a good description of these functions.

A key issue in this work is the relationship between illuminance and contrast threshold. It is apparent from Figs 5 and 7 that neither Weber's nor square-root law provided good descriptions of this relationship. To characterize these data better, we calculated the slopes of the log contrast threshold vs log illuminance functions exhibited by each adult, 2-month old, and 3-month old for each spatial frequency tested. Specifically, the function $t = k * i^n$ (t is contrast threshold, i is illuminance, and k and n are constants) was fit to the data. Figure 8 shows the exponents n of these best-fitting lines; the exponents correspond to slopes in the log–log plots of Figs 2–7. Exponents of 0.0 and -0.5 correspond to Weber's and square-root law respectively. Figure 9 shows the average exponents as a function of spatial frequency for the three age groups tested.

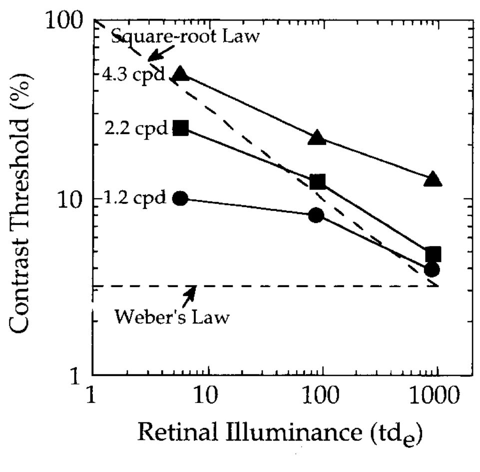

FIGURE 7. Average 3-month data. Average contrast thresholds are plotted as a function of retinal illuminance. The horizontal axis represents equivalent trolands. The data points represent averages from 11 3-month olds at spatial frequencies ranging from 1.1 to 4.4 c/deg. Square-root and Weber's law are indicated by the dashed lines.

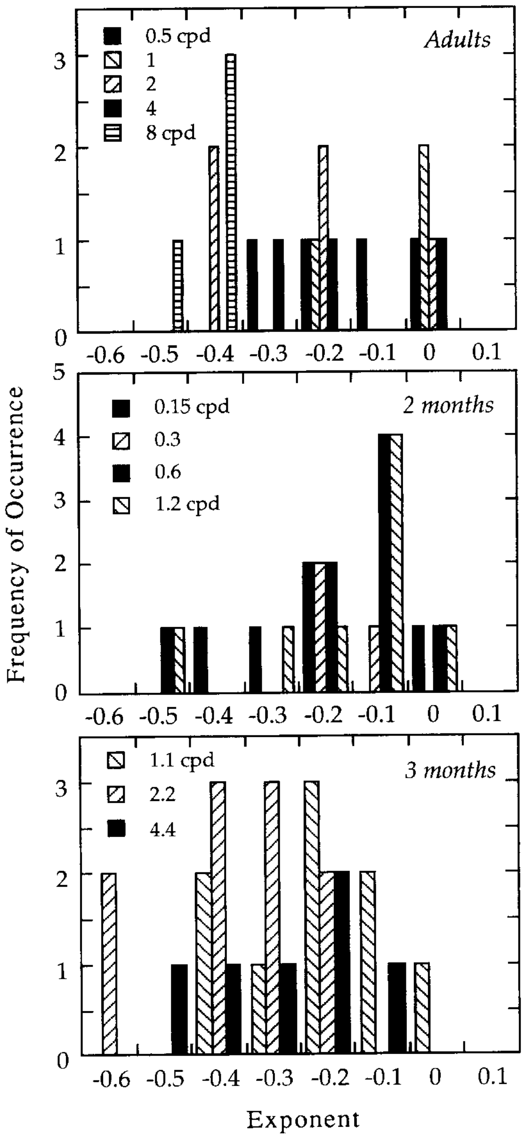

FIGURE 8. Slopes of contrast threshold vs illuminance curves. The data were fit with the equation $t = k * i^n$, where t is threshold, i is illuminance, k and n are constants. The three panels display the best-fitting exponents n for 2- and 3-month olds and adults. Exponents are plotted separately for different spatial frequencies. Square-root law is represented by an exponent of -0.5 and Weber's law by an exponent of 0.

The adult data exhibited the expected variation of slope with spatial frequency (van Nes & Bouman, 1967), steeper slopes occurring at higher frequencies. There is no clear evidence for a similar slope increase among the infants. There is also no obvious age-related change in slope at a given spatial frequency.

Fiorentini *et al.* (1990) measured contrast thresholds in one 2 1/2-month old at 0.06 and 6 cd/m^2. We fit their

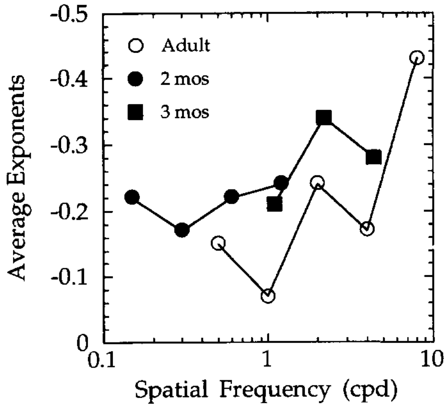

FIGURE 9. Average slopes of contrast threshold vs illuminance curves at different spatial frequencies and age. The exponents were estimated as described in the caption to Fig. 8.

data as described above and found that the exponents of the best-fitting power functions were between 0 and -0.5 (-0.21 at 0.4 c/deg, -0.24 at 0.7 c/deg, and -0.45 at 1 c/deg). Thus, our data from a larger population are in general agreement with those of Fiorentini *et al.* (1990).

DISCUSSION

These are the first comprehensive measurements of the relationship between contrast sensitivity and retinal illuminance in infants. As pointed out in the Introduction, such measurements are important for three reasons: (1) evaluating the dark glasses hypothesis for a task that is not constrained by as many factors as resolution tasks; (2) determining how much reduced photon catch ought to affect contrast sensitivity in order to evaluate previous modeling approaches (Banks & Bennett, 1988; Banks & Crowell, 1995; Brown, 1990; Wilson, 1988, 1995); and (3) determining whether spatial frequency channels in infants behave like adult channels at the same spatial frequency or at a higher spatial frequency as hypothesized by Wilson (1988, 1995). We discuss each of these issues here.

Dark glasses hypothesis

We know that the photon catch in the infant's retina is reduced in comparison to the mature retina; the reduction is most marked in the fovea. Does this reduction alone account for the reduced contrast sensitivity observed early in life? The data reported here are an important first step in answering this question. By knowing the relationship between illuminance and contrast threshold at the ages of interest, we can now ask whether infant and adult contrast thresholds can be rendered similar by elevating the illuminance presented to infants (or reducing the illuminance presented to adults). Figure 10 displays 2-month and adult contrast threshold vs illuminance functions at 2–2.2 c/deg and Fig. 11 displays 3-month and adult functions. Naturally, infant thresholds were higher than adult thresholds, more so at 2 than at 3 months.

Can a reduction in infants' photon catch reasonably explain the differences between infant and adult contrast thresholds? One can answer this question by shifting the infant data along the log illuminance axis (which mimics the effect of increasing the photon catch). In Figs 10 and 11 we have shifted the infant data in this fashion to obtain the best fit to the adult data. An enormous shift of 2000-fold was required to render the 2-month and adult data at 2 c/deg similar while smaller shift of 120-fold rendered the 3-month and adult data similar.* Therefore, we can confidently reject the reduced photon catch model at this spatial frequency for 2-month olds because the required shift is much larger than the actual reduction in the photon catch (Banks & Bennett, 1988; Wilson, 1988). We cannot, however, reject the model for 3-month olds because the required shift may be similar to the reduction in photon catch. Unfortunately, we cannot determine how accurately the reduced photon catch model accounts for the 3-month data because there are currently no quantitative anatomical data available for that age from which an estimate of the reduction in photon catch could be obtained. Thus, the contrast thresholds of 2-month olds are higher than expected from an analysis of the sensitivity losses due to reduced photon catch, but the thresholds of 3-month olds might by explained in this fashion.

Evaluation of modeling assumptions

Recall that Wilson (1988, 1995) assumed square-root law (slope $= -0.5$) in predicting the contrast threshold elevations that accompany a reduction in photon catch

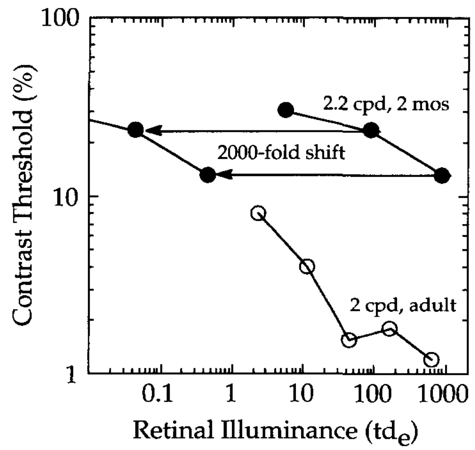

FIGURE 10. Shift required to match adult and 2-month thresholds at 2 c/deg. The average 2-month data at 2.2 c/deg and the average adult data at 2 c/deg are plotted as a function of retinal illuminance. The infant data are also shifted horizontally by a factor of 2000 to fit the adult data.

*There is some evidence that extrafoveal retina in neonates is relatively more mature than the fovea (Hendrickson & Drucker, 1992). The modeling efforts cited and used here are based on measurements of foveal receptor and lattice properties. Is it possible that the conclusions would differ had we modeled extrafoveal retinal properties instead? It seems unlikely that it would affect the conclusions because extrafoveal retina is relatively more rather than less mature and therefore receptor and lattice properties would, if anything, constrain contrast sensitivity less than we have modeled.

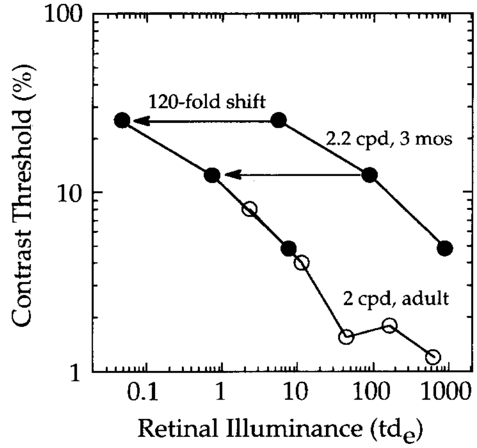

FIGURE 11. Shift required to match adult and 3-month thresholds at 2 c/deg. The average 3-month data at 2.2 c/deg and the average adult data at 2 c/deg are plotted as a function of retinal illuminance. The infant data are also shifted horizontally by a factor of 120 to fit the adult data.

and Banks and Bennett (1988) assumed square-root law for spatial frequencies of 4 c/deg and above and shallower slopes for low spatial frequencies. The data in Figs 5 and 7 show quite clearly that Wilson's assumption is incorrect for 2- and 3-month-old infants for spatial frequencies of 0.15–2.2 c/deg; the slopes are without exception shallower than predicted by square-root law. The data also show that Banks and Bennett's assumption is incorrect for 3-month olds at 4 c/deg because here too the slope was shallower than predicted by square-root law. The data also show that the modeling assumption Brown (1990) applied to the increment threshold paradigm is not valid for contrast thresholds with sinusoidal targets because the slopes are steeper than Weber's law. The same exercise conducted at 1 c/deg leads to a similar conclusion: An implausibly large shift factor is required to fit the 2-month data and a smaller, more plausible one is sufficient to fit the 3-month data.

We can now re-examine the modeling efforts of Banks and Bennett (1988) and Wilson (1988, 1995) using empirically-derived estimates of how much changes in illumination ought to affect infants' contrast sensitivity. In both modeling efforts, the consequences of reduced eye size, coarser receptor spacing, smaller receptor apertures, and reduced optical density (among individual receptors) on spatial contrast sensitivity were estimated given certain modeling assumptions. To make predictions about infant CSFs, one must assume optical transfer functions and numerical apertures for infant eyes as compared to adult. Banks and Bennett and Wilson assumed adult-like optical transfer functions and numerical apertures. One must also assume what the properties of the photoreceptor lattice are. Unfortunately, we do not have quantitative anatomy on the retinas of 2-month olds. The only quantitative data (Yuodelis & Hendrickson, 1986) come from a newborn and a 15-month eye. Banks and Bennett (1988) constructed ideal discriminators with the properties of the newborn and 15-month eyes. They claimed that the photon catch of the newborn fovea was 1/350 that of the adult and that the catch of the 15-month fovea was 1/4.7. If we assume that the relationship between age and the photon catch reduction can be described by $r = m * e^{na}$ where r is the ratio, a is age in months and m and n are constants (this is tantamount to assuming that the logarithms of the ratios change linearly with age), we estimate a catch reduction of 1/200 at 2 months. This is admittedly quite speculative, but in the absence of quantitative anatomical data from 2-month eyes, it is better than simply substituting the newborn or 15-month value for 2-month olds.

Banks and Bennett (1988) and Wilson (1988, 1995) modeled the effect of reduced photon catch by assuming square-root law, so by this argument 2-month CSFs should be similar to adult CSFs except for a $\sqrt{1/200}$ reduction. We have shown the effect of this shifting in Fig. 12. The solid symbols represent the adult and 2-month CSFs obtained at the highest luminance tested. The two functions with open symbols represent the adult CSF shifted downward by different amounts. The lower function was produced by shifting the adult function by $\sqrt{1/200}$ and notice that the predictions actually fit the infant VEP data reasonably well. The problem is that the square-root law assumption now seems unjustified: infants' contrast thresholds are less affected by illuminance changes than predicted by square-root law. The upper function reflects a more realistic assumption; it was produced by shifting by the amounts determined in the experiment reported here. Stated another way, we determined the vertical shift factors at each spatial frequency by using the slope of the appropriate contrast threshold

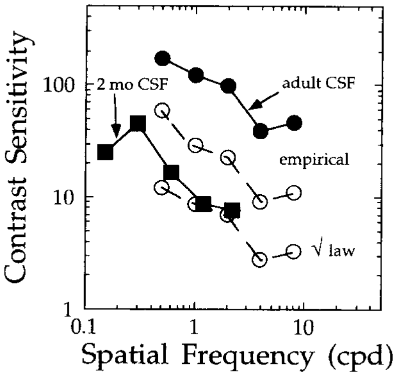

FIGURE 12. Predictions of reduced photon catch models. CSFs are plotted for adults and 2-month-old infants. Adult CSFs at 70 cd/m^2 which correspond to an illuminance of about 636 td; these data are also displayed in Fig. 3. ■ 2-month CSFs at 70 cd/m^2 which corresponds to an illuminance of about 911 equivalent td; these data are also shown in Fig. 5. The dashed lines and ○ represent predictions of reduced photon catch models for two different assumptions concerning the relationship between illuminance and contrast sensitivity. The lower function shows the prediction if square-root law is assumed; specifically, it shows the adult CSF once shifted downward by $\sqrt{200}$. The upper function represents the prediction if the values we derived experimentally are used; i.e. it shows the adult CSF once shifted downward by the changes in contrast sensitivity that are associated with an illuminance reduction of 200 (see Fig. 5). The shift factors were $200^{0.21}$ at 0.5 c/deg and $200^{0.29}$ at the higher frequencies.

vs illuminance function (Fig. 5) to determine how much shift in contrast threshold would occur with a 200-fold reduction in photon catch. The model prediction falls short of explaining the low contrast sensitivity of 2-month olds across a broad range of spatial frequencies.

As one would expect from Fig. 11, a similar exercise for the 3-month data is less conclusive. The formula above yields an estimated photon catch reduction of 1/145. Using the data from the present experiment to shift adult CSFs vertically yields a reasonable fit to observed 3-month CSFs. So if the photon catch is really reduced by a factor of 1/145 in 3-month olds, the observed reductions in contrast sensitivity may well be consistent with the dark glasses hypothesis. This observation is not definitive, however, because there are no quantitative anatomical data on 3-month-old eyes from which one could estimate the actual reduction in photon catch.

Figure 12 illustrates the utility of the data reported here in modeling the effects of front-end immaturities on infants' spatial vision. This analysis also highlights the importance of obtaining quantitative anatomical data in the age range between birth and 15 months so that we can better estimate the photon catch loss at different ages.

Does the preferred spatial frequency of spatial channels shift with age?

Wilson (1988) hypothesized that the preferred spatial frequency of spatial channels increases substantially with age as a consequence of the centripetal migration of cones during the first few years of life. Specifically, a channel tuned to 2 c/deg at birth ought to be tuned to 9 c/deg in adulthood. High-frequency channels in adults follow square-root law up to higher illuminances than do low-frequency channels, so one might predict from Wilson's hypothesis that a 2-c/deg channel in early infancy should be more likely to exhibit square-root law like a 9- rather than a 2-c/deg channel in adulthood. We

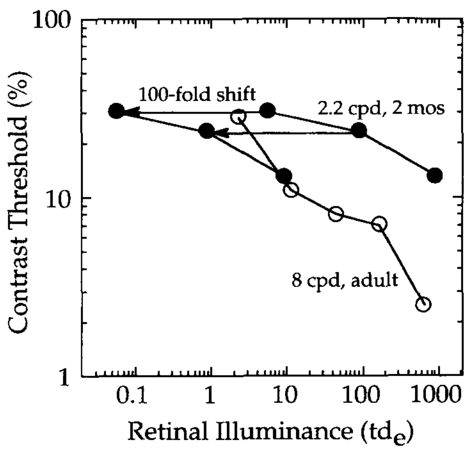

FIGURE 13. Shift required to match 2-month thresholds at 2.2 c/deg to adult thresholds at 8 c/deg. The average 2-month data at 2.2 c/deg and the average adult data at 8 c/deg are plotted as a function of retinal illuminance. The infant data are also shifted horizontally by a factor of 100 to fit the adult data.

evaluated this hypothesis by comparing infant thresholds at 2.2 c/deg to adult thresholds at 8 c/deg. Figure 13 plots contrast threshold as a function of retinal illuminance for infants at 2.2 c/deg and adults at 8 c/deg. The infant data have also been shifted along the log illuminance axis to fit the adult data. Although a smaller shift factor was required, one can see that the fit was actually poorer than the one in which we fit infant and adult data at the same spatial frequencies (Fig. 10). This comparison provides modest evidence that low-frequency channels in infants do not behave like high-frequency channels in adults, at least in terms of their adaptive properties. This evidence, however, does not disconfirm Wilson's hypothesis because it is clearly possible that the spatial frequency tuning and adaptive properties of spatial channels both change with age.

CONCLUSION

We used the sweep VEP to measure the relationship between retinal illuminance and contrast sensitivity at different spatial frequencies in adults and 2- and 3-month-old infants. As one might expect, contrast threshold fell with increasing illuminance at all ages and spatial frequencies. The exponents required to fit the contrast threshold vs illuminance functions were similar in infants and adults at a given spatial frequency. Exponents obtained in infants were generally less than predicted by square-root law for the range of spatial frequencies tested. Thus, the square-root law assumption made in previous models of infant spatial vision (Banks & Bennett, 1988; Wilson, 1988, 1995) is disconfirmed. Once the models are modified to incorporate the relationship obtained in the present experiment, the predictions fall well short of explaining 2-month olds' low contrast sensitivity, but they may or may not be consistent with 3-month olds' low sensitivity.

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